

XIV. *On the Agamic Reproduction and Morphology of Aphis*.—Part I. By THOMAS H. HUXLEY, F.R.S., Professor of Natural History, Government School of Mines. Communicated by G. BUSK, F.R.S., F.L.S.

Read November 5th, 1857.

- § 1. Preliminary Remarks.
- § 2. The Viviparous Female, and the Development of the Pseudova.
- § 3. The Oviparous Female, her Reproductive Organs and Ova.
- § 4. The Development of the Pseudovarium in the Viviparous Female.
- § 5. Summary; and Comparison of Germs and Ova.
- § 6. Hypothetical Explanations of Agamogenesis.
- § 7. Classification of the Phenomena of Agamogenesis.

§ 1. *Preliminary Remarks.*

“J’AI souvent pensé qu’on pourrait, dans l’histoire des sciences, désigner les époques par les principales découvertes. Par exemple, 1665 seroit *l’époque de la Gravitation*; 1789, *l’époque de la méthode naturelle en Botanique*; et, *si parva licet componere magnis*, les années 1740 à 1750 seroient *l’époque des Pucerons*\*.”

Without, perhaps, being disposed to go so far as the enthusiastic French investigator of Plant-lice, no physiologist will deny that the experiments conceived and attempted by Réaumur, but first successfully carried out by Bonnet, established facts of the highest importance, and raised questions which still disturb the very foundation of his science.

But what were these great facts, established by Bonnet and his successors or contemporaries, Trembley, Lyonet, Degeer, Kyber, and others?

If the moderns paid due attention to the labours of their predecessors, an accurate answer to this question should be found in every accredited text-book on zoology. But it will be found, on the contrary, that important errors have crept into the current conceptions respecting the reproductive processes and mode of life of the *Aphides*, and that at the present day the state of general information as to the natural history of these singular creatures is in many respects rather behind, than in advance of, that of the past generation.

Bonnet’s wonderfully patient and laborious researches† proved, beyond all doubt, 1st, that the viviparous *Aphis* may propagate without sexual influence; 2ndly, that the brood thus produced may give rise to young in the same way; that these may repeat this asexual proliferation; and so on for as many as ten broods; 3rdly, that the viviparous *Aphides* and their brood may be either winged or apterous; 4thly, that, under certain conditions, winged or wingless males appear and copulate with oviparous females, which, in the instances observed by Bonnet, were wingless.

These are the statements put forth by Bonnet on the evidence of direct observation

\* Duvau, Mém. du Muséum, xiii. 1825.

† Traité d’Insectologie, 1745.

and experiment, and they have been confirmed by every subsequent original observer whose works I have perused. Besides these matters of fact, Bonnet states, as his strong opinion, that there is no fixed limit to the process of agamic, viviparous reproduction, and that, under favourable conditions of warmth and nourishment, it might be continued for "thirty generations" (*l. c.* p. 102), or, in other words, indefinitely.

The accurate and pains-taking Degeer, who gives an elaborate account of some seventeen species of *Aphis*, affirms as the result of his researches, "that the winged *Aphides* are never oviparous\*." He describes at length the apterous males of certain species (*P. lisse du Pin*, *P. du Pommier*, *P. du Genévrier*), and shows that apterous, oviparous, and winged viviparous broods may coexist, as in *Aphis Rosæ*.

Degeer considers that, as a general rule, the oviparous females and the males are produced by alate viviparous females.

The next important original memoir on the *Aphides* is that published in Germar's *Magazin der Entomologie* for 1815, by Kyber†, evidently a most careful observer, but somewhat wanting in method and clearness as a writer. Kyber is in perfect accordance with Bonnet and Degeer; and more than this, he experimentally proved the justice of Bonnet's supposition, that the duration of the agamic reproductive power is practically indefinite, and is chiefly, if not wholly, dependent on conditions of temperature and nutrition. He says (p. 34):—

"I never saw a male in copulation with a winged female in any species. It was always the apterous females which were attacked by the males; for in many species apterous females remain among the families. Neither have I ever seen winged females lay eggs. This has, indeed, been already remarked by Degeer."

In a note Kyber adds the caution, that he has not observed more than twenty species in copulation, and does not wish to extend his conclusions beyond these.

The fourth note to this important paper contains the following remarkable observation:—....."The winged females especially, in which, even after frost has set in, fully-formed young may always be found, when the apterous females of the same family have long been laying eggs. On the 21st November, 1812, I still had winged *Aphides* (*Haberblattläuse*) in my possession, although the apterous ones had copulated and laid their eggs in September,—a remarkable circumstance without doubt, and one whence important conclusions with regard to the mode of propagation of the *Aphides* are likely to flow. Possibly, many winged females survive the winter together with their young." (p. 10.)

In other parts of his memoir (p. 2 *et seq.*), Kyber adduces strong evidence in favour of the hibernation of the viviparous forms of some species; which Degeer had already proved to be the case with respect to the remarkable "*Puceron des Galles du Sapin*."

In the *Aphis Dianthi*, Kyber was never able to observe either copulation or oviposition; and so far from there being any natural term to the number of asexual broods which succeed one another, he states that he raised viviparous broods of both this species and *A. Rosæ* for four consecutive years, without any intervention of males or oviparous

\* Degeer, *Mém. sur les Insectes*, 1774, vol. iii. p. 74.

† Einige Erfahrungen und Bemerkungen über Blattläuse von J. F. Kyber, Diacon. in Eisenberg.

females, and that the energy of the power of agamic reproduction was at the end of that period undiminished. The rapidity of the agamic proliferation throughout the whole period was directly proportional to the amount of warmth and food supplied.

Duvau, in his already cited "Nouvelles Recherches sur l'histoire naturelle des Pucerons," read before the French Academy of Sciences in 1825, states that he had carried the series of successive agamic generations in the *Aphis* of the Bean (fève) to *eleven*, which was one more than Bonnet had obtained. The process lasted seven months, and the last young was born on the 27th December, but died on the 29th. Duvau, however, kept some alive until January, and naturally asks whether it is not probable that, under favourable circumstances, the agamic process may be continued throughout the winter. The average length of life of his *Aphides* was thirty days, or a little more; but the representative of the ninth generation lived from September 29th to December 19th, or eighty-one days. Like those of preceding observers, Duvau's researches clearly show the influence of temperature on the fecundity of the viviparous *Aphis*.

It is in Morren's in many respects valuable paper on the *Aphis Persicæ*, published in the 'Annales des Sciences Naturelles' for 1836, that the germs of the two most notable errors which have crept into the natural history of the *Aphides* may be found. At p. 76 the following passage occurs\* :—

"The influence of temperature on these animals is obvious; in other *Aphides*, and under ordinary circumstances, the female lays her eggs when she has wings and after copulation with the male, who is winged at the same epoch. Oviposition takes place in this manner at the seventh generation for some—at the ninth or even at the eleventh for others; before it, female larvæ alone are produced."

Morren here supposes himself to be simply repeating what he has read. But so far as I am acquainted with the older literature of the *Aphides*, he is entirely mistaken. I can nowhere discover that either Réaumur, Bonnet, Degeer†, Kyber, or Duvau have observed winged oviparous females in any species; nor do the statements of any of these observers justify the belief that the sexual forms always appear after a certain number of generations. All that Bonnet affirms is, that his particular experiments came to an end accidentally after the production of a certain number of agamic generations, which is, of course, quite another matter.

When Morren details his own observations, his results are in exact accordance with those of the older observers. "In the *Aphis Persicæ*," says he, "I have very frequently seen (and I have shown the phenomenon to my colleague, M. Burgrove) that the winged and fertilizable female never contained ova and never laid any, but that she contained little living *Aphides*, which are born fully developed, and provided with legs, proboscis, and

\* "L'influence de la température sur ces animaux est manifeste; chez les autres pucerons, et dans les circonstances ordinaires, la femelle pond des œufs lorsqu'elle est ailée, et après un accouplement avec le mâle ailé à la même époque. Cette ponte se fait ainsi à la septième génération pour les uns, à la neuvième ou même à la onzième pour les autres; avant elle, il y a seulement naissance de femelles naissant à l'état de larves."—Morren, *l. c.*

† Degeer's account of the gall-forming Puceron du Pin is an apparent exception to this statement, but I believe only an apparent one. Degeer expressly states that he never saw the winged form of this species in copulation; and, besides, it is not a true *Aphis* at all.



antennæ. It was only in November that the apterous females presented eggs in their ovaries and oviducts, and for that effect, a considerable degree of cold was necessary\*."

Morren describes the male, female, and agamic organs of reproduction, but less completely than Von Siebold, who, in 1839†, carefully investigated the *Aphis Lonicerae*, and first demonstrated the existence of the spermatheca and colleterial glands in the oviparous females. Von Siebold distinguishes three forms of this species, two winged and one apterous. The large winged *Aphides* were all viviparous; the smaller, males. The apterous forms were oviparous, and the progeny of the alate females.

Steenstrup says of the *Aphides* (Alternation of Generations, p. 108), "The propagation of these creatures through a series of generations has been already long known. In the spring, for instance, a generation is produced from the ova, which grows and is metamorphosed, and without previous fertilization gives birth to a new generation, and this again to a third, and so on for ten or twelve weeks; so that in certain species even as many as nine such preliminary generations will have been observed; but at last there always occurs a generation consisting of males and females, *the former of which* after their metamorphosis are usually winged; fertilization and the depositing of eggs take place, and the long series of generations recommences in the next year and in the same order."

In the first edition of Professor Owen's 'Lectures on the Invertebrata,' published in 1843, however, Morren's errors are adopted, extended, and enunciated as the law of propagation of the *Aphides*, in the following terms:—

"In the last generation, which is the seventh, the ninth, or the eleventh, according to the species of *Aphis*, the fertilizing influence would seem to have expired‡, and developmental force exhausts itself in more frequent and numerous moultings, in the formation of wings, and in the modification of the female organs already described. Many males, which, like the females, acquire wings, form part of the produce of the last brood, which takes place in autumn. They rise in the air, frequently migrate in incalculable numbers, unite, and the females then produce eggs, which are glued to twigs and leaf-stalks, retain their vitality throughout the winter, are hatched in the spring, and give birth to the apterous and larviparous females, which continue to produce successive generations of similar females until the close of summer." (p. 235.)

It has not been my good fortune to discover, either in Prof. Owen's writings or those of his predecessors, any evidence in support of the singular statement contained in the last paragraph of this citation, which is incorrect in all important respects, and has, indeed, been omitted in the second edition of the 'Lectures.'

Mr. Walker, in the first of his long and valuable series of papers on the *Aphides* (Annals, vol. i. 1848, p. 259), writes thus:—

\* "Or chez le puceron du pêcher j'ai vu un grand nombre de fois, et j'ai montré le phénomène à mon collègue, M. Burgræve, que la femelle ailée et propre à la fécondation ne renfermait point des œufs et n'en pondait point, mais qu'elle renfermait des petits pucerons vivants qui naissent tout développés avec leurs pattes, leur trompe, et leurs antennes. Ce ne fut qu'en Novembre que les femelles sans ailes présentaient des œufs dans les ovaries et les oviductes, et pour cela il fallait un froid déjà assez vif."—Morren, *l. c.* p. 76.

† Ueber die inneren Geschlechtswerkzeuge der viviparen und oviparen Blattläuse. Friep's Neue Notizen, 1839.

‡ This phrase is little more than a translation of a passage in Morren which will be given below.



"I am indebted to my friend Mr. Haliday for the following translation of an extract from Erichson's Bericht, &c., 1844, Ent. Zeitung, pp. 9, 81, 133, 410. Ratzeburg observed a species of *Aphis* on the Birch, which continued to produce a living progeny from August into winter without either male or female appearing. Bouché and Kaltenbach, in explanation, remark that the males in this family are not always winged. However, in the May following, Ratzeburg, continuing his observations, found the winged females, and afterwards (in October) winged males also, which paired with them. The species was then identified as *A. oblonga*, Von Heyden. For the male to pair with a winged female (continues Mr. Walker) is a very unusual case among *Aphides*\*." In fact, I have hitherto found, in Mr. Walker's long list of 101 species, no case of an oviparous winged female observed by himself. Mr. Walker states as a known fact, that *Aphis Rosæ* habitually lives through our mild winters.

In his work on 'Parthenogenesis' (1849), Prof. Owen modifies his previous statement so far as to say, in a note (p. 59), that the perfecting of the female generative organs in *Aphis* "is not attended by the acquisition of wings; or if they be developed in the oviparous female, they soon fall. I have, however, retained them in the diagram for a better illustration of the analogy. Many of the virgin viviparous *Aphides* acquire wings, but never perfect the generative organs."

The diagram referred to exhibits two figures, (*h*) and (*i*), which, for anything that appears in the text, might be taken to be the author's representation of male and female *Aphides*. On comparing them with the illustrations of Morren's memoir, however, it is at once obvious that they are copies of his figures 1 and 2, of which fig. 2 does really represent a male; while fig. 1, on the other hand, is not an oviparous, but a viviparous female. In the explanation of his figures, Morren indeed merely says of fig. 1, "Femelle vue en dessous;" but it requires no great amount of attention to his text to observe his distinct statement (already quoted), that the winged female is viviparous, and not oviparous. I am obliged to be thus particular in explaining these unusual circumstances, as otherwise the existence of a typical figure of a winged oviparous female *Aphis*, in the work of an accredited author, might be brought forward as conclusive evidence of the ordinary occurrence of such females†.

\* On turning to Ratzeburg's notice in the 'Entomologische Zeitung,' 1844, p. 410 (Fortgesetzte Beobachtungen über die Copula der Blattläuse), which is the last word of the correspondence between Kaltenbach, Bouché and himself on this subject, I find his precise words to be these:—"Wie gross war daher mein Erstaunen, als ich bei meiner ersten, nach der Rückkehr angestellten Excursion, am 22 October gleich auf den ersten Blick unter der Menge von ungeflügelten Individuen, welche die des vorigen Jahres bei weitem übertraf, auch geflügelte Puppen und geflügelte Männchen bemerkte, und wie gross war meine Freude, auch gleich darauf mehrere der letztern in der Begattung zu finden, also in einem Acte, den ich bei Blattläusen selbst noch nicht hätte beobachten können." Subsequently, Ratzeburg states that he was able to observe the copulatory process early and late, at any time between the 22nd October and the 16th November.

It will be observed that there is not a word here about such winged females as Ratzeburg, in a preceding passage, states he saw in May of the same year. The winged pupæ are apparently, from the context, the pupæ of the males, and the forms with which the winged males copulated were the wingless females. So that here, as in all other supposed cases of winged, oviparous true *Aphides* I have looked into, the evidence, when closely examined, breaks down.

† Professor Owen, in the last edition of his 'Lectures on the Invertebrata,' p. 410, quotes Léon Dufour as having witnessed the coitus of the male *Aphis* "with the winged female." The reference is to "Dufour, Léon, in Annales

When the natural history of the *Aphides* is freed from the mythical additions which have accumulated around, and obscured it, I believe the following propositions may be said to be established on good evidence:—

1. Ova deposited by impregnated female *Aphides* in autumn are hatched in the spring.
2. From these ova, viviparous, and in the great majority of cases apterous, forms proceed.
3. The broods to which these give rise are either winged or apterous, or both.
4. The number of successive broods has no certain limit, but is, so far as we know at present, controlled only by temperature and the supply of food.
5. On the setting in of cold weather, or in some cases on the failure of nourishment\*, the weather being still warm, males and oviparous females are produced.
6. The males may be either winged or apterous.
7. So far as I am aware, there is no proof of the existence of any exception to the law that the oviparous female is apterous.
8. Viviparous *Aphides* may hibernate, and may co-exist with oviparous females of the same species.

So much by way of clearing the ground. I now proceed to the particular subject of this paper, which is primarily, to describe the nature of the process by which the agamic young arises within the body of its viviparous parent. But very few investigators have applied themselves to this question, and those who have are unfortunately in diametrical contradiction to one another as to the most important points.

Prof. Leydig published a notice on this subject in the 'Isis' for 1848, which I have not seen; but subsequently his views, fully stated and accompanied by figures, were promulgated in Siebold and Kölliker's *Zeitschrift* for 1850, vol. ii. Heft 1. He maintains "that the germ of the (viviparous) *Aphis* is developed out of cells, and its embryo is as much composed of cells as one which has proceeded from a fecundated ovum" (*l. c.* p. 65). And he particularly details the manner in which one of the large cells contained in the terminal chamber of the proliferous organ of the viviparous *Aphis* becomes detached, enlarges, and is converted into the embryo. Although Leydig does not absolutely say as much, his observations lead to the conclusion that there is no histological difference between the agamic germ in its youngest state, and a true ovum at a corresponding period.

Von Siebold implies, and Prof. Owen, Victor Carus, and the late Dr. Waldo Burnett assert, with different degrees of distinctness, on the contrary, that there is a clear histolo-

des Sciences Naturelles, vol. i. 1844.' I have carefully, and more than once, scrutinized this volume of the 'Annales,' without having been able to discover the passage referred to. Léon Dufour has, in fact, two memoirs in the first volume of the 'Annales' for 1844. The first is on the "Anatomie générale des Diptères;" the second, "Histoire des Métamorphoses et de l'Anatomie du *Piophilæ Petasionis*." As might be expected, there is no reference to the *Aphides* in either of these papers.

Finally, the authors of the article "Hémiptères" in the 'Suites à Buffon' (1843), p. 600, quote De la Hire as their authority for saying that the oviparous female *Aphis* is winged. I have examined the passage cited (*Histoire de l'Acad. Royale des Sciences*, 1703), however, and I find only this:—

"M. de la Hire *croit* que les pucerons vivent une année entière, et que pendant l'hiver ils se retirent dans des trous, d'où ils sortent au printemps pour pondre leurs œufs, comme le font les mouches ordinaires."

\* See Hausmann's "Beiträge" in Illiger's *Magazin*, Bd. 2.

gical difference between the primary germs of the viviparous *Aphis* and true ova,—Carus and Burnett reiterating their opinions even since the publication of Leydig's views. Finally, Mr. Lubbock, in his late valuable memoir on *Daphnia*, (Phil. Trans. 1857) has expressed his inability to find any germinal vesicle in the germs of the viviparous *Aphis*, and, so far, may be ranked among Leydig's opponents.

I have recently resumed some investigations commenced two or three years ago on this interesting subject. My object was originally purely morphological,—the *Aphis* suggesting itself as a very convenient subject for working out the general development of *Insecta*; but I have found myself unable to refrain from wandering out of my direct course, and attempting to further the solution of the great problem of Agamogenesis, or asexual reproduction.

My observations are in the main in accordance with those of Leydig. On many minor points, however, we are at variance; and besides this, there are matters of great interest, upon which Leydig does not touch, but on which I hope to be able to throw some light. For, besides yielding an answer to the question as to the existence or absence of any histological distinction between a bud and an ovum, the investigation of the viviparous and oviparous *Aphides* affords decisive evidence as to the soundness of certain explanations of the phenomena of Agamogenesis in general; and finally, the study of the general development of *Aphis* furnishes data of great importance in Articulate Morphology.

I propose in the present memoir to follow out these lines of inquiry. I will in the first place describe the minute structure of the essential reproductive organs or "Pseudovaria" of the viviparous or agamic female; and the development of its germs or pseudova (as I propose to term them) will be considered. Secondly, the reproductive organs of the oviparous female and the development of the ova will be described. Next, I shall speak of the manner in which the proliferous apparatus or pseudovarium of the viviparous female is developed within the germ; and I shall compare together the agamic and sexual reproductive processes. I shall then endeavour by means of these facts to refute a hypothesis which has been offered in explanation of Agamogenesis; and finally, I propose to consider the Morphology of the *Articulata* so far as it is elucidated by Development.

The species of *Aphis*, the reproductive organs of whose viviparous form I am about to describe, appeared this autumn upon a plant of the Ivy-leaved Geranium which hangs in my study, and for the last two months has been regularly giving rise to broods, sometimes winged and sometimes apterous, without any appearance of males or females. With respect to the external characters of the reproductive organs, I have nothing of importance to add to Siebold's or Morren's description.

## § 2. *The Development of the Pseudovarium.*

The terminal chamber of any of the cæca of the pseudovarium is a rounded or oval body (Pl. XXXVI. fig. 1, A), united by a delicate ligament (*a*), proceeding from its free end, with the ligaments which pass from the other cæca of the same side, to form the common pseudovarian ligament. The wall of the chamber is a delicate transparent membrane (*b*), in which, here and there, rounded endoplasts (or nuclei) are imbedded; while others lie on its inner



side, constituting a sort of epithelial layer (*c*) continuous with the contents of the chamber. These, when perfectly unaltered, are constituted by a homogeneous pale periplastic substance (*d*), containing about a dozen clear spheroidal cavities (*e*) whose walls are a little denser than the rest of the periplast. The cavities have on an average a diameter of  $\frac{1}{3000}$ th of an inch. In the centre of each is a rounded opaque body (*f*) like one of the endoplasts of the wall of the dilatation, and, indeed, obviously of the same nature.

In whatever fluid I have examined this tissue, it began after a time to alter. In the very weak syrup which I ordinarily employed, the change consisted partly in the slightly increased definition of the walls of the clear cavity, but more particularly in the breaking up of the periplast into spheroidal masses, each of which contained a single vesicle and its endoplast\*. The resemblance of such a body to an ovum with its germinal vesicle and spot is complete; nor would it be possible for any one ignorant of the origin of the body to say that it was other than an ovum. Water instantly alters the appearance of the tissue, completely destroying its distinctive character. Dilute glycerine shrivels up the vesicles and alters the appearance of their central endoplast, probably by endosmose. Acetic acid renders the periplast dark, and gives an exceedingly marked definition to the parietes of the vesicle. To see the appearances I have described as normal, the part must be examined perfectly fresh, and in a solution of sugar neither too dilute nor too concentrated.

In certain specimens the contents of the lower part of the terminal chamber are different from those of the upper. As much as a third of the whole chamber may be occupied by a mass of periplast containing only a single clear vesicle. Such a condition is figured in fig. 1, Pl. XXXVI. Fig. 2 exhibits a further advance in the same direction; the mass, which, from its close resemblance to a true ovum, I have called a pseudovum, having enlarged so much as nearly to equal the contents of the terminal chamber, from which it is distinguished by a slight constriction. In figs. 3 and 4, the constriction has become more marked, until at length a penultimate chamber is formed, connected only by a narrow neck with the terminal one, fig. 4. It is on an average about  $\frac{1}{500}$ th of an inch in diameter. The epithelial layer (*c*) of its wall is ordinarily well developed, and when water is added swells up, so as to separate the periplastic substance of the pseudovum from the wall. The periplast itself exhibited no structure, and appeared unchanged except in size. The clear vesicle was sometimes unchanged, sometimes enlarged, but otherwise unaltered. Of its endoplast I was sometimes unable to discover any trace; on other occasions I found a few granules in its place (fig. 3); and, once, two particles, each rather more than half its diameter, appeared to lie side by side in the interior of the vesicle.

The marked contrast between the perfect distinctness of the endoplast in the vesicles contained in the ultimate pseudovarian chamber, and its apparent absence in the very similar vesicle of the mass contained in the penultimate chamber, or in the lower part of the last one, was the more striking, as the two could be readily compared under the same circumstances and in the same field of view.

\* Leydig (*l. c.* p. 63) appears to regard this as the first state of the ovigerms, and he has overlooked the epithelium.

Finally, the vesicle itself ceases to be visible (fig. 4), and the penultimate chamber contains only its epithelium and a mass of apparently structureless substance;—I say apparently structureless, because the addition of water made the mass more clear, and at the same time rendered an irregular arcolation and scattered granules visible in its substance. Whether the areolæ are the outlines of delicate vesicles, and the granules their endoplasts, or not, are points which I could not satisfactorily determine; at any rate, I could never observe anything like the regular structure observable in the contents of this chamber when a little larger.

Fig. 5 represents such a chamber,  $\frac{1}{417}$ th of an inch in length. The endoplasts of the wall are seen lying in or upon it, and occupying its interior is a distinct oval mass of substance agreeing in appearance with the periplast of the pseudovum, but distinguished from it by containing a great number of clear spheroidal cavities not more than  $\frac{1}{3200}$ th of an inch in diameter, each of which contains a central endoplast of not more than  $\frac{1}{10000}$ th of an inch. These cavities are closely packed, but not flattened against one another. The walls of the cavities react differently on the addition of acetic acid to the rest of the periplast, becoming darker and more sharply defined. In fact, each cavity is what is commonly termed a nucleated cell, while the intervening periplast is the so-called intercellular substance.

I have here stated merely the histological facts which may be observed by any one who will take the trouble to examine with sufficient care the ultimate and penultimate pseudovarial chambers of a few viviparous *Aphides*. Of the existence of these states, and that the order in which I have detailed them fairly represents the order in which they succeed one another in nature, I have no doubt; and I therefore look upon it as an established fact, that the primary steps in the agamic development of *Aphis* are, first, the enlargement of the periplast around one of the pseudovarian vesicles, and its detachment as a separate body, which, from its resemblance to an ovum, I will call a "pseudovum;" secondly, the contemporaneous formation of a distinct chamber—the penultimate chamber of the pseudovarium; thirdly, the disappearance of the vesicle of the pseudovum, and the conversion of the latter into a germ-mass composed of cells imbedded in intercellular substance and containing minute endoplasts.

I should be sorry, however, to express an opinion as to the exact nature of the process by which these changes are effected, with anything like the same degree of confidence. Three hypotheses present themselves:—

1st. The pseudoval endoplast divides and subdivides, so as to give rise to the endoplasts of the germ; or—

2nd. The pseudoval endoplast is resolved, and the endoplasts of the germ are developed autogenously in its periplast; or—

3rd. The pseudoval endoplast disappears, and the endoplasts of the germ are supplied from the epithelium of the walls of the pseudovarial chamber.

Of these three hypotheses, I strongly incline towards the first, as most in accordance with what we know of histological development in general. The whole progress of modern research, in fact, goes to show that cells and endoplasts hardly, if ever, arise autogenously, but are the result of the subdivision of pre-existing cells and endoplasts. If

this be the case, however, the second hypothesis is excluded, and the third is improbable in itself, and is supported by no evidence. In the absence of such evidence, the marked contrast in size and appearance between the epithelial endoplasts of the penultimate chamber and those of the germ tends to show that the two have no direct relation to one another.

Those who have followed the details of the development of the pseudovum and its resulting germ, given above, will not fail to admire the clear insight of Morren, when he affirmed that the agamic offspring of *Aphis* was developed by "the individualization of a previously organized tissue." A more neat and expressive definition of the process could not be given: and as Morren nowhere entertains the absurd doctrine that an organized tissue must be as complex as "mucous membrane" or "muscular fibre," which has been attributed to him, the criticisms to which his views have been subjected on this ground are sufficiently baseless. No one will pretend to deny that the pseudovarium is "organized," nor that the pseudovum is a portion of it which has become "individualized." But I subjoin Morren's words, that the reader may form his own judgment as to his merits:—

"A dire vrai, je me refuse à émettre une opinion au milieu d'un tel dédale, et je tiens pour plus philosophique d'avouer son ignorance dans un phénomène où la nature nous refuse même l'apparence d'une explication. S'il fallait une explication à toute force, j'admettrais que la génération se fait ici comme chez quelques entozoaires, *par individualisation d'un tissu précédemment organisé*. La génération n'est pas pour cela spontanée: une *génération spontanée* doit être la production d'un être organisé de toutes pièces, lorsque les élémens inorganiques se réuniront pour produire un animal, une plante. Cette génération est impossible et n'a jamais lieu. Une *génération équivoque* est celle où des tissus organisés préalablement par un être déjà pourvu de vie, s'individualisent, c'est à dire, se séparent de la masse commune et participent encore, après cette séparation de l'état dynamique de la masse, c'est à dire, de sa vie, mais à son propre profit. C'est ainsi qu'un tissu produit un entozoaire\*. C'est de la vie continuée. Mais supposez que la vie ait assez d'énergie pour imprimer au tissu que s'individualise la forme de l'espèce productrice, et vous avez la génération des pucerons. Cette énergie se perd au bout de quelques générations, et une nouvelle impulsion devient nécessaire, c'est celle du mâle.

"Voilà à tout hasard, une hypothèse que dans ma jeunesse j'aurais embrassée avec plaisir; mais aujourd'hui je préfère douter: les faits que j'ai exposés plus haut valent mieux qu'une théorie."—Morren, sur le Puceron du Pêcher, Annales des Sc. Nat. série 2. vi. 1836, p. 90.

### § 3. *Description of the Oviparous Female Aphis and of the Development of the Ovum.*

Throughout the two months during which the Ivy-leaved Geranium, on which my viviparous *Aphides* are living, has been in my possession, neither males nor females have

\* I need hardly remark, that no evidence of the development of *Entozoa*, in the way supposed by Morren, is in existence.



made their appearance. Therefore, being extremely desirous to compare the process of the development of the germ with that of the ovum, before completing this paper, I began in the last days of October to seek for oviparous females of some other species.

An Oak-tree in the Zoological Gardens at length supplied me with that which I sought. The small twigs and leaves afforded habitation to a number of minute wingless *Aphides*, all so nearly equal in size, that I did not doubt their non-viviparous, and hence in all probability their oviparous character.

Microscopic examination fully confirmed my suspicions; for not only were the *Aphides* full of ova, but I found multitudes of similar ova adhering to the plant in the axils of the leaves, and more particularly between the outer bracts of the buds\*.

These *Aphides* were very different from my viviparous species. They were about  $\frac{1}{12}$ th of an inch in length. The general hue of the body was pale green; but it was diversified in the dorsal region by four longitudinal rows of blackish rounded spots, one spot in each row being seated on the tergum of most of the somites, from the prothorax backwards. Hence, there were nearly as many transverse rows of four spots each, as segments of the body. The two median spots in each row were larger, and situated close to the middle line. The external spots were more upon the sides of the body. The spots upon the mesothorax, and thence to the sixth abdominal somite inclusive, were the largest and most conspicuous. Each spot was constituted by a dark elevation of the integument, which supported a tuft of long setæ, knobbed at their extremities like the glandular hairs of certain plants. The hairs were not confined to these localities, however, but were scattered over the head and other parts of the body. The eyes were red, and produced into a small tubercle on their posterior margins. The distal portions of the antennæ, and the tarsi, were blackish. The antennæ were not more than equal to half the body in length; they were seven-jointed, the penultimate joint being somewhat swollen at its extremity. Both this and the preceding and following joints were so sculptured as to appear, at first, minutely annulated. The basal joint was the thickest of all, the second less thick, but stronger than the others. The proximal half of the antennæ was sparsely setose. The promusculis was short, extending, when deflexed, no further than the posterior edge of the prothoracic sternum. The abdomen tapered into a cone beyond its sixth somite, on whose dorso-lateral region the very short trumpet-mouthed siphons were situated. The abdomen was terminated by two subcylindrical rounded setose tubercles, of which the lower was the larger. They had the anus between them, and acted as anal valves. The posterior limbs, when fully extended, hardly reached beyond the end of the abdomen.

The eggs when first laid are of a dark green hue and very soft; afterwards they appear to become black.

The vulva of the oviparous *Aphis* (B) opens between the eighth and ninth abdominal sterna, the eighth (8) being a little prolonged, so as to form a sort of inferior lip to the vaginal aperture (Pl. XL. fig. 1). The vagina (C) is a thick-walled tube provided with a

\* I do not think that my *Aphis* of the Oak is identical either with that described by Réaumur, or that described by Bonnet. None of my specimens attained the size of theirs, nor do either of those writers mention the peculiar dorsal markings of my species: furthermore, the proboscis in both Réaumur's and Bonnet's was long; in mine it is very short. The proper specific names of both the *Aphides* alluded to in this memoir will be discussed in a final note.

layer of external transverse, and internal longitudinal, striated muscles. After entering the sixth abdominal somite, it divides into two branches—the oviducts (DD), whose walls exhibit the same muscularity, but are less thick. Both vagina and oviducts are lined by a well-developed epithelium.

The oviducts divide into four ovarian cæca, whose delicate structureless wall is unprovided with muscles, and lined by a columnar epithelium. Each cæcum is ordinarily divided by constrictions into six chambers. Of these I found the posterior (that nearest the vulva) (E) always empty, and of nearly the same length, though of a much smaller diameter than that which precedes it, or the fifth from the apex of the ovarium. This fifth chamber (F) always contained a fully formed ovum, provided with a chorion and an opaque coarsely granular yolk.

The fourth chamber (G) is smaller than the fifth; it contains a coarsely granular vitelline mass in which no germinal vesicle can be perceived, and which ordinarily has no investing membrane.

The third chamber (H) is still smaller; and its contents are usually only slightly granular, so that the germinal vesicle and spot of the ovum in this chamber are beautifully distinct (fig. 2).

The second chamber (I) is the smallest of all; the germinal vesicle and spot of its rudimentary ovum can be easily seen; and but very few fine granules are deposited in the substance which will eventually form the yolk.

A clear cord-like mass (*q*), commonly divided longitudinally, so as to appear double, traverses this chamber, and can be traced into the next.

The apical chamber (K) is as large as the third, but is longer transversely than longitudinally, while the reverse is the case with the third chamber. Its outer wall is formed by a continuation of the same structureless membrane as that which constitutes the rest of the cæcum. The epithelium (*p*), which is particularly thick in the upper part of the second chamber, especially at the neck or constriction between the first and second, is suddenly attenuated as it spreads on the inner face of the wall of this chamber, and becomes very thin from the flattening of its cells. From having the characters of a cylinder-, it takes those of a pavement-epithelium.

It is at first extremely difficult to understand the nature of the contents of the apical chamber. All its anterior part appears to be filled with about a dozen closely appressed bodies (*l*), which, if examined without due attention, or under a low power only, may easily be confounded with ova. Each of these bodies has a sort of wedge shape, such as would result from the compression of rounded masses in a spherical envelope which they nearly fill. Its apex is turned inwards; its base outwards. Each consists of a thick transparent outer coat closely investing a denser and well-defined membranous sac. The latter contains a clear substance, in which many irregular granules are imbedded. The lines of separation between the appressed sides of these bodies are well seen, either in a sectional or a superficial view. In the latter case, they appear as polygonal meshes; in the former, as lines separating the bodies from one another, and bounding their curved bases on the side of the epithelium. On tracing the lines of separation towards the central interval between the ends of these bodies, they become lost, and a mere clear, homogeneous

substance seems to occupy the whole central part of the chamber; but on carrying the eye backwards, this clear mass is seen to be continuous with the two cords which I have above described as entering the second chamber (Pl. XL. fig. 3).

The histological constitution of these bodies is at once sufficient to convince the observer that they are not ova, and I regard them as glandular masses which secrete the matter of the clear cord-like bodies which descend into the second and third chamber.

The ova themselves, or rather the rudiments of the future ova, are not always to be seen with ease; and if the epithelium of the lower part of the apical chamber has become much altered, they cannot be detected: for they are visible exclusively in this part of the chamber, of whose epithelial cells they are, as I believe, merely a modification. However this may be, germinal vesicles and spots of all sizes intermediate between that of the ovum of the second chamber and that of an ordinary epithelial cell are seen in close contact with the parietes of the chamber. I have detected as many as six in this position. When the chamber is subjected to compression they may be set free, and are then seen to be surrounded by a zone of clear substance, the rudimentary vitellus. Under similar circumstances, the "glandular bodies" may also be isolated; when they present themselves as vesicles surrounded by a clear homogeneous substance, which is frequently prolonged at their apical extremity. It is gradually dissipated, and the inner sac set free by the action of water.

I have not seen any ovarian ligament in the oviparous *Aphis*.

The structure which I have described was wholly unexpected and new to me; and I am not aware that anything similar has yet been noticed in the ovaria of Insects\*. I am inclined to believe that the glandular bodies contribute directly to the formation of the vitellus, because I have more than once seen cases, like that figured in Pl. XL. fig. 3, where the clear cord-like body appeared to pass directly into the mass of the ovum. There was always a widely open communication between the first and second, and between the second and third chamber; but the passage between the third and fourth was closed by the meeting of the epithelial lining. Does each ovum, as it is given off from the ovary, and passes backwards, carry with it a gelatinous mass, the product of one half of the glandular bodies, and only cease to be connected with these glands when it has taken the third place?

Three cæca open into the dorsal side of the lower part of the vagina; of these the anterior single one is the spermatheca, the posterior pair are the colleterial glands (Pl. XL. fig. 1, *m*, *n*).

The spermatheca (*n*) is a sac with a narrow neck, dilated at its extremity, which opens considerably in advance of the colleterial glands, while its enlarged end lies between them. The duct of the spermatheca has thick walls continuous with those of the vagina; but its dilated portion is thin, and has a yellowish colour. It contains a multitude of large filiform spermatozoa bent upon themselves, and is very tough and resisting.

The colleterial glands (*m*) are subcylindrical, but are constricted inferiorly where they

\* Unless, as I am strongly inclined to suspect from Leydig's description, and from a hasty examination on my own part of the ovaria of *Coccus*, the corresponding chamber of that insect's remarkable ovaria presents a similar structure. (See, however, the note which concludes this paper.)



open close to the vulva. They consist of a delicate structureless coat lined by a thick layer of granular substance, whose cellular composition is very indistinct in the fresh state, but becomes obvious on the addition of acetic acid.

The interior of the gland contains a clear, viscid, strongly-refracting substance, apparently separated from the epithelial lining by a membranous layer. I am in doubt, however, whether this apparent membrane be anything more than the folded and wrinkled outer layer of the viscid matter. When the *Aphis* is suddenly placed in glycerine or subjected to slight pressure, a drop of the colleterial secretion not unfrequently exudes and manifests its viscosity by leaving a long trail.

The fully-formed ovum (Pl. XL. fig. 1, F) measures about  $\frac{1}{70}$ th of an inch in length. It is oval, rather smaller anteriorly, and of a deep green hue, in consequence of the colour of the yelk. The chorion is a tough transparent membrane, about  $\frac{1}{9000}$ th of an inch thick, and presents no external sculpturing or internal structure. Internal to the chorion is a delicate vitelline membrane which immediately invests the yelk. It is, however, connected with the chorion posteriorly. When the egg is heated with caustic potass, the yelk is driven away from the sides (eventually dissolving), and with it the vitelline membrane on the sides and at the anterior part of the ovum; posteriorly, however, I always found it adherent. The yelk itself is very coarsely granular; so that there would be no chance of discovering the germinal vesicle, even if it existed.

The recent observations of Leuckart and Meissner on the micropyle of the ovum in Insects naturally induced me to look for such a structure in the egg of *Aphis*.

Leuckart, in his elaborate essay, clearly shows that the micropyle may be single or multiple, and may occur at either or both poles of the egg; but unfortunately he gives us less information respecting the ova of the Homopterous *Hemiptera* than regarding those of any other great group of Insecta. *Cercopis*, in fact, is the only genus of this division in which he has observed the micropyle with certainty, and here there are two, one on each side of the anterior pole.

The anterior extremity of the chorion in *Aphis* (Pl. XL. fig. 4, B) presents a small conical papilla, in which I have been unable to discover any aperture. Internally, however, the corresponding surface of the chorion appears as it were rough and uneven; and when caustic potass is added, it, like the rest of the inner surface of the chorion, exhibits a very curious marking, as if so many circles or more irregular figures were impressed upon it. The thickness of the papilla is about  $\frac{1}{4000}$ th of an inch; and in young ova a delicate filiform appendage more than once appeared to be continuous with it: this, however, was invariably absent in fully-formed ova.

At the opposite pole (fig. 4, A), the ovum presents a curious appendage, about  $\frac{1}{530}$ th of an inch in length. When the ovum is in its natural position within the ovary, the epithelium of the latter, which closes over it below, leaves a sort of chamber in which this appendage, ordinarily more or less closely applied against the chorion, is received.

When the ovum is extracted, the appendage appears like a rope with loosened strands, or a closely-plaited membrane, and is seen to be coated with a clear gelatinous substance, in which many minute rod-like filaments of about  $\frac{1}{4000}$ th of an inch in length are imbedded. Treated with caustic potass, this clear substance and its imbedded particles are

dissipated, and the central cord becomes less distinct; but I have never yet seen it dissolved, and sometimes it seems altogether to resist the reagent. The rounded tubercle of the chorion to which it is attached, however, now clearly exhibits a central funnel-shaped body, continuous with the axis of the appendage, and appearing like a canal (fig. 4, C).

Is this a micropyle, and what is the nature of the appendage? I regret that I have not the leisure to pursue the inquiry far enough to answer this question satisfactorily; but I incline to think that the micropyle is really situated here\*.

The albuminous papilla surrounding the bundle of spermatozoa in the impregnated ova of *Musca*, *Dexia*, and *Melophagus* (Leuckart, *l. c.* pl. 7. figs. 1, 2, 4, 5), reminds one strongly of the envelope of the appendage in *Aphis*.

The micropyles of *Libellula*, *Dexia*, and *Musca*, again, exhibit a sort of "mouthpiece" formed by a prolongation of the chorion surrounding the micropylar aperture.

The account which I have given of the reproductive organs of the oviparous *Aphis* is in general agreement with that of other observers. Morren describes the reproductive organ of the wingless oviparous female of *A. Persicæ* thus:—

"The ovigerous cæca well deserved their name; for no foetuses were any longer visible in them. Each was exactly composed of three chambers, of which the first or terminal was enlarged and spherical, and filled with twelve to twenty-four little, well-formed ova, yellow in the centre, and white peripherally. These ova descended into the second chamber, and then elongated and enlarged; but in general they acquired their hard covering only in the third or last chamber, which in all the females was occupied by a very large ovoid greenish ovum. These ova became covered at the same time with the sebific liquid; for some were seen to be provided with a little appendage intended to fix them to the bodies in which the parent lays them. This appendage was mucous, and arose from a thickened viscous liquid." (*l. c.* p. 89.)

I recognize in Morren's "twelve to twenty-four ova" the ovarian glands which I have described. His microscope was obviously inadequate to show him the true ova; but it seems difficult to suppose that in this species there is, as he maintains, neither colleterial glands nor spermatheca. His objection to Dutrochet's statements appears to me to be well founded, for Dutrochet examined a viviparous female; but I strongly suspect that he has himself overlooked the "sebific" apparatus in the oviparous forms.

Von Siebold states that the ovarian cæca of the oviparous *Aphis Lonicæræ* are divided into only two chambers:—

"In the undeveloped state the whole tube forms only a simple pyriform appendage of

\* After describing the cup-like micropyle at the anterior pole of the ovum of the Louse, Leuckart (*l. c.*) goes on to say—"Besides this micropylar apparatus at the anterior pole, there is at the posterior pole of the ovum a structure which attracts attention. It may be described as a blunt cone, which is attached rather on one side of the centre of the posterior pole, and has acquired a peculiar striated appearance by reason of its longitudinal folds, and band-like thickenings. The interior diameter of this structure measures  $\frac{1}{8}$ ''' ; the upper is less, about  $\frac{1}{8}$ ''' ; and the length is about the same. A hollow space is contained within this body, so that it might be compared to a bell; but it seems as if from the roof, or cupola, as it might be termed, of this bell, a number of closely appressed elevations and points depended. With respect to the import of this remarkable apparatus, I will only throw out the supposition that it is an apparatus of attachment. For a long time I thought I had discovered in it a second micropylar apparatus; but I renounced this view when I was unable to discover any aperture in it." (p. 140.)

the oviduct; but as development proceeds, the upper globular chamber becomes by degrees separated by a constriction, and at the same time a great difference makes its appearance between the upper and the lower chambers: for the lower chamber contains a finely granular mass which gradually becomes modelled into an oval egg; the upper chamber, on the other hand, is filled with vesicular bodies, in which smaller vesicles containing a nucleus are distinguishable. If these bodies are to be regarded as germs of ova (Wollte man diese blasenförmigen Körper als Eier-keime betrachten), we may assume that these *Aphides* were capable of bringing forth more than eight ova."

Von Siebold then goes on to describe the colleterial glands, and the spermatheca, which had not before been seen. If the ovaries of *Aphis Lonicerae* are not constructed on a totally different plan from those of the species I have described, it is, I think, pretty clear that Von Siebold, like Morren, has mistaken the ovarian glands for the rudiments of the ova. Indeed, his phraseology indicates that he himself had no great confidence in his interpretation of the parts.

#### § 4. *The Development of the Pseudovarium.*

In the viviparous female, the germ increases in size, and gradually becomes separated from the terminal chamber by the successive development and separation by constriction of new pseudova. The number of chambers between the terminal one and that nearest the vagina, therefore, varies until it attains its maximum, which is necessarily regulated by the ratio between the time required for the perfection and birth of a larva, and the rate at which new pseudova are detached from the pseudovarium. In the species of *Aphis* which I examined, I found ordinarily four or five such chambers. Germs between  $\frac{1}{400}$ th and  $\frac{1}{250}$ th of an inch in length presented the following characters (Pl. XXXVII. fig. 1):—They exhibit a central darkish matter, surrounded by a clear cortex. The latter is composed of a single layer of a substance similar in appearance to that composing the mass of the germ above described, while the central substance is obscured by a number of minute granules which hide its internal structure. Nevertheless, I have occasionally detected what I believe to be endoplasts, scattered through its substance, as in Pl. XXXVII. fig. 1, which represents a germ in this stage treated with very dilute acetic acid; and as in a more advanced condition we shall find such bodies easily recognizable, I do not doubt that the central substance has the same fundamental composition as the peripheral layer. The central mass, it will be observed, completely simulates the vitellus of an impregnated ovum; and I will therefore term it a "pseudovitelus." The peripheral clear layer is, on the other hand, in all essential respects comparable to a blastodermic vesicle; and I see no reason why it should not be called a blastoderm, since the term is not necessarily confined to the product of impregnation.

In a more advanced condition (fig. 3), the blastoderm has become thicker in all parts, so as to consist of at least two or three layers of "cells;" but the thickening shows itself especially upon one side of the distal end of the germ (that turned towards the vagina), where the blastoderm is nearly twice as thick as in other parts. A linear demarcation appears in the midst of this thickened layer (fig. 4); and at the same time indications of a separation are traceable between the distal extremity of the thickened portion and the rest of the blastoderm: it is as if the latter were giving way at this point. In some



specimens the cell-cavities of the inner portion of the thickening were particularly well marked; and the coarsely granular central substance exhibited a tendency to break up into large globular masses, which became particularly distinct on the addition of water.

It is in the largest of these germs that the resemblance of the pseudovum to an ovum is completed by the formation of a pseudovitelline membrane (fig. 3, *a*). This structureless homogeneous membrane is, doubtless, developed by a process of excretion, either from the pseudovum or from the walls of the chamber which contains it. It completely envelops the pseudovum, and acquires greater thickness and strength as development proceeds.

The embryo first becomes clearly fashioned in pseudova between  $\frac{1}{200}$ th and  $\frac{1}{150}$ th of an inch in length (Pl. XXXVII. fig. 5). At the distal extremity, in the region of the thickening of the blastoderm, the latter appears separated into two portions, the outer of which forms a sort of hood over the inner. The hood eventually becomes the hinder part, if not the whole, of the abdomen of the larva. It is continuous, on the side answering to the dorsal side of the larva, with the rest of the blastoderm, which now, instead of enclosing the pseudovitellus, lies partly beneath and partly behind it. That portion of the blastoderm which lies behind the pseudovitellus, and parallel with the hood, is the rudiment of the sternal region of the thorax; and I shall hereafter term it the thoracic segment of the blastoderm. That part of the blastoderm which lies beneath the pseudovitellus will become the sternal region of the head; and I shall therefore call it the cephalic segment, while the hood itself is the abdominal segment of the blastoderm.

The thoracic segment, it will be observed, is in this stage bent up at right angles to the axis, and reaches the dorsal region, which it bounds posteriorly. The cephalic segment, on the other hand, hardly extends upwards at all, but lies in one plane; so that the anterior end of the embryo is almost wholly formed by the pseudovitellus. The latter is aggregated into a few large globular masses, which are in immediate contact with the pseudovitelline membrane on their dorsal surface.

The pseudovitellus is in immediate contact inferiorly with a layer of the blastoderm of a more pellucid aspect than the rest, and separated from it by a more or less distinct line of demarcation. This layer (*q*) could be detected only on the dorsal face of the thoracic and cephalic segments, and owed its superior transparency to the comparatively large size of the clear cavities surrounding its endoplasts.

That portion of the layer which covered the posterior portion of the thoracic segment was particularly remarkable for the size and clearness of its cells and their endoplasts (*r*). In the progress of development, the central portion of the alimentary canal occupies a place nearly corresponding to the centre of the clear layer; while, if we trace out the site of the rest of the mass in larger and larger embryos (Pl. XXXVIII. figs. 1, 3, 4, 5), we find it always retaining the same relative position to the reflected abdominal hood, but gradually enlarging, and eventually becoming subdivided into five oval lobes upon each side, each of which surrounds itself with a membrane, and assumes the form of the terminal chamber of one of the pseudovarial caeca. It would be a great mistake to suppose that it is only one of these chambers, however; it is in fact the rudiment of an entire caecum; and before the embryo leaves the parent, it becomes divided into three chambers by the gradual development and metamorphosis of pseudova in the way described above.

The granular pseudovitellus takes no part whatever in the formation of the reproductive organs. In embryos of  $\frac{1}{8}$ th of an inch in length, I could very plainly observe a clear space with an endoplast in the middle of each of its spheroidal masses (Pl. XXXVIII. fig. 3). Similar masses constitute a larger or smaller proportion of the corpus adiposum of the larva and adult insect; and I believe that the latter proceeds from the former.

### § 5. *Summary and Comparison of Germs and Ova.*

I will now sum up the results of the observations which have been detailed in the preceding pages.

1. The pseudovarium consists of vagina, oviducts, and pseudovarian cæca.
2. The vagina is unprovided with either spermatheca or colleterial glands.
3. The pseudovarian cæca are each divided into many chambers by constrictions.
4. The apical chamber contains bodies which are not distinguishable from the germinal vesicles and spots of the true ovaria.
5. These bodies, surrounded by a mass of clear substance representing a yolk, are set free as pseudova, and are then undistinguishable from true ova.
6. The pseudova are eventually converted into cellular germs, apparently by the same process as that by which an ovum is converted into an embryo.
7. In these germs the central part becomes a granular pseudovitellus, the peripheral a blastoderm; the rudiments of the different organs next appear, and the germ becomes surrounded by a pseudovitelline membrane.
8. Eventually the pseudovitellus probably becomes the corpus adiposum.
9. All the other organs are developed from the blastoderm, which becomes distinguished into two layers. From the outer of these the muscles, nerves, limbs, and tegument are developed, while the inner gives rise to a part of the alimentary canal (?) and to the reproductive organs or pseudovarium of the larva.
10. The pseudovarium contains no particle of unchanged tissue of the germ, but is a considerably differentiated and readily distinguishable mass. The mass divides into ten lobes anteriorly; and these lobes become the pseudovarian cæca. Before the larva is born, each cæcum is divided into three chambers, the two posterior of which contain rudimentary embryos.
11. The genital apparatus of the oviparous female consists of a vagina, oviducts, and ovarian cæca. The latter are multilocular; and the vagina is provided with the spermatheca, and the two colleterial glands first demonstrated by Von Siebold.
12. The rudiments of the ova are undistinguishable from those of the pseudova. They are developed in the lower part of the apical ovarian chamber, the upper part of which is occupied by the bodies I have termed ovarian glands. The ova are not at first enveloped in a chorion.
13. In the lowest chamber the ova are provided with a chorion, vitelline membrane, and what appears to be a micropyle.

If these propositions are correct, I see no valid objection to the conclusion, that the agamic offspring of *Aphis* is developed from a body of precisely the same character as that

which gives rise to the true egg. The pseudovum is detached from the pseudovarium in the same way as the ovum from the ovarium. In both cases, the act of separation is in every respect a process of gemmation.

From this point onwards, however, the fate of the pseudovum is different from that of the ovum. The former begins at once to be converted into the germ; the latter accumulates yelk-substance, and changes but little. Both bodies acquire their membranous investment rather late; within it the pseudovum becomes a living larva, while the ovum is impregnated, laid, and remains in a state of rest for a longer or shorter period.

Although, then, the pseudovum and the ovum of *Aphis* are exceedingly similar in structure for some time after they have passed out of the condition of indifferent tissue, it cannot be said that the sole difference between them is, that the one requires fecundation and the other not. When the ovum is of the size of a pseudovum which is about to develope into an embryo, and therefore long before fecundation, it manifests its inherent physiological distinctness by becoming, not an embryo, but an ovum. Up to this period the influence of fecundation has not been felt; and the production of ova instead of pseud-ova must depend upon a something impressed upon the constitution of the parent before it was brought forth by its viviparous progenetrix.

In this respect, the ova of *Aphis* exhibit the same relation to the pseudova as the ephippial eggs of *Daphnia* (whose development has been so well described by Mr. Lubbock) bear to the agamic eggs; for the histological change in the ovarium of *Daphnia*, which precedes the development of the ephippial eggs, is clearly shown by Mr. Lubbock to have no relation to fecundation.

Let me remark on yet another interesting, though perhaps only partial, analogy. Von Siebold has shown that the ova of the Queen bee produce females or males, according as they are fecundated or not. The fecundated ovum produces a queen or a neuter according to the food of the larva and the other conditions to which it is subjected; the unfecundated ovum produces a drone. Now, what have we seen in *Aphis*? The fecundated egg produces viviparous *Aphides*, which are the equivalents of the neuter bees; and from them are eventually produced males and oviparous females. The oviparous females are fecundated and lay eggs which produce only viviparous or neuter *Aphides*.

On the view which Dr. Carpenter and myself take of the zoological individual, the whole produce of a single fecundated ovum of the *Aphis* is as much the *Aphis* individual as it is the Bee individual. Consequently we have two equivalent and related series.

## I.

## II.

Bee. Impregnated ova	} producing	Neuters or females	} producing	Ova requiring impregnation, and males.
Aphis. Impregnated ova		Viviparous neuters		Females which give rise to ova requiring impregnation, and males.

The fact that in the one case the males are developed from pseudova resembling fully-formed true ova, and in the other from pseudova resembling imperfectly-formed ova, makes no essential difference in the analogy, but only demonstrates still more clearly the impossibility of drawing any absolute line of demarcation histologically between ova and buds.



§ 6. *Hypothetical Explanations of Agamogenesis.*

The majority of writers on the wonderful phenomena of Aphidian life, have been content to state the facts more or less clearly; but Morren, who has done this so clearly and philosophically, has in addition carelessly thrown out a hint of a mode of explaining them. The agamic *Aphis*, he says, is a portion of organized tissue which individualizes itself:—

“Suppose that vitality is sufficiently energetic to impress, on the tissue which individualizes itself, the form of the producing species, and you have the generation of the *Aphides*. This energy becomes lost at the end of a certain number of generations, and a new impulse becomes necessary. It is that of the male. In my youth I might have adopted with pleasure such an hypothesis as this; but now I prefer to doubt: the facts which I have set forth are worth more than a theory.”

The hypothesis is, however, to my mind, in no essential particular distinguishable from that hypothetical explanation which has been propounded by the author of the well-known work on “Parthenogenesis.” Substitute for “energy of the male,” in the foregoing passage, “spermatic force;” and the difference between the two hypotheses becomes evanescent.

But this is a question of minor importance as compared with the value of the hypothesis in itself; and it is with regard to this latter point that I now propose to make a few remarks.

Professor Owen’s views are, I believe, fairly stated in the following extracts from the work cited:—

“We find derivative germ-cells, and masses of nuclei like those resulting from the final subdivision of germ-cells, retained unchanged at the filamentary extremities of the branched uterus forming the ovaria of the larval *Aphides*.”—*l. c.* pp. 7, 8.

“According to my own observations, the germs are perceptible in the embryo *Aphis*, above the simple digestive sac, before any organs have been formed for their reception. And with regard to the nature of the organs when formed, I may remark that the continuity of the ovarian tubes with the oviducts in all insects, is such as to render the negation of the term ‘ovary’ to those two bodies from which the slender extremities of the eight oviducal and uterine tubes proceed in the larval *Aphis*, to say the least, quite arbitrary. My examinations agree with those of Siebold, in determining scarcely any appreciable difference between the ovaria of the oviparous and those of the viviparous females. The contents of the ovarian tubes differ, inasmuch as they contain oval masses of granules or nuclei, comparable to the germ-mass in its state of minutest subdivision, in the virgin *Aphides*, and not ova with the germinal vesicle as in the oviparous females.”—*Ibid.* p. 38.

“The completion of an embryonic or larval form by the development of an ovarian germ-cell, or germ-mass, as in the *Aphis*, without the immediate reception of fresh spermatic force, has never been known to occur in any vertebrate animal.

“The condition which renders this seemingly strange and mysterious generation of an embryo without precedent coitus possible, is the retention of a portion of the germ-mass

unchanged. One sees such portion of the germ-mass taken into the semitransparent body of the embryo Aphis, like the remnant of the yolk in the chick. I at first thought that it was about to be enclosed within the alimentary canal, but it is not so. As the embryo grows, it assumes the position of the ovarium, and becomes divided into oval masses and enclosed by the filamentary extremities of the eight oviducts..."—*Ibid.* p. 69–70.

"It would be needless to multiply the illustrations of the essential condition of these phenomena. That condition is, the retention of certain of the progeny of the primary impregnated germ-cell, or in other words, of the germ-mass unchanged, in the body of the first individual developed from that germ-mass, with so much of the spermatie force inherited by the retained germ-cells from the parent cell or germ-vesicle as suffices to set on foot and maintain the same series of formative actions as those which constituted the individual containing them."—*Ibid.* p. 72.

"The physiologist congratulates himself with justice when he has been able to pass from cause to cause, until he arrives at the union of the spermatozoon with the germinal vesicle as the essential condition of development—a cause ready to operate when favourable circumstances concur, and without which cause these circumstances would have no effect.

"What I have endeavoured to do has been to point out the conditions which bring about the presence of the same essential cause in the cases of the development of an embryo from a parent that has not itself been impregnated. The cause is the same in kind, though not in degree, and every successive generation, or series of spontaneous fissions, of the primary impregnated germ-cell, must weaken the spermatie force transmitted to such successive generations of cells.

"The force is exhausted in proportion to the complexity and living powers of the organism developed from the primary germ-cell and germ-mass."—*Ibid.* pp. 72, 73.

These statements are repeated in the recently published second edition of Prof. Owen's *Lectures on the Invertebrata*.

The paragraphs I have cited contain two kinds of propositions—assertions with respect to matters of fact, and deductions from those assertions. The former are, according to my observations, incorrect; and, as I conceive, the latter are unfounded.

As regards the first citation, for instance, the contents of the apical chambers of the pseudovaria are *not* by any means identical with those "resulting from the final subdivision of germ-cells retained unchanged," as the most cursory comparison of the two structures will show.

In the second citation it is affirmed that the germs are perceptible in the embryo before any organs are formed for their reception. This, again, is an error if my observations are correct. The absence of figures, and the too vague and general character of the descriptions in Prof. Owen's work, render it very difficult to understand what he really has seen; but I imagine that he has taken the substance which constitutes the rudiment of the whole pseudovarium, and which becomes differentiated partly into pseudova, partly into the walls of the organ, for a mass of germs. What is meant by "those two bodies from which the

slender extremities of the eight oviducal and uterine tubes proceed," and which are supposed to be ovaries, I am at a loss to divine. There are no such bodies, that I can discover.

In the latter part of the same citation, the existence of a histological difference between the contents of the pseudovarium and those of the ovarium is asserted. But there is assuredly nothing in the former to which the description can apply; and I re-affirm the impossibility of drawing any histological line of demarcation between the pseudova and the young true ova.

How any one who carefully studies the development of *Aphis* can arrive at the conclusion that a portion of the germ-mass is taken into the body of the embryo *Aphis*, "like the remnant of the yolk of the chick," I know not; and, for the reasons mentioned above, I even doubt if I clearly apprehend what is meant. Dr. Burnett (*l. c.* p. 73) assumes that what is intended by "portion of the germ-mass" is what I have termed the pseudovitellus. In that case the statement is erroneous; for the pseudovitellus takes no share in the formation of the pseudovarium. If, on the other hand, the true rudiment of the pseudovarium is indicated, the statement in question is equally incorrect; for this is never out of the body, and hence can hardly be taken into it, nor can that out of which the so-called "oviducts" are produced be properly said to become "connected with them," or to "aid in forming their filamentary extremities."

When the basis of a hypothesis is shown to be incorrect, the hypothesis itself is commonly considered to be disposed of; but possibly in the present case it may be urged that, although the contents of the pseudovarium *are* wholly dissimilar "to the germ-mass in its state of minutest subdivision," they are nevertheless so little changed that my criticism of the phrase is trivial. To this I reply that, whether the alteration be small or great, it is *as* great as that which occurs in the terminal cæca of a gland, or in a true ovarium, and that the tissue of the apical pseudovarian chamber is far more differentiated than the indifferent tissue which constitutes the youngest portion of an ordinary epithelium or epidermis.

Whatever conclusions are based upon the resemblance of the tissue of the pseudovarium to that of the embryo, must therefore apply in equal or greater force to the tissues which I have just named; and, unless reason can be shown to the contrary, whatever powers are possessed by the one, in virtue of this similarity, must be possessed in equal or greater degree by the other.

But in this case what becomes of the hypothetical explanation of the asexual reproduction of *Aphis*, under discussion?

The condition of such reproduction is, according to the hypothesis, the retention of "certain of the progeny of the primary impregnated germ-cell unchanged," "with so much of the spermatie force, inherited by the retained germ-cells from the parent-cell or germ-vesicle, as suffices to set on foot and maintain the same series of formative actions as those which constituted the individual containing them."

Let us imagine, for the sake of argument, that the amount of histological change in the pseudovarian mass is unimportant. I am ready to suppose even, in accordance with the hypothesis, that its cells retain sufficient "spermatie force" (whatever that may be)



to commence an independent life. But I ask, how does this explain agamogenesis? Why does not the epithelium of the ovary (which is as little or less changed) give rise to young without impregnation? Why are not the young cells of glands, which are as little changed, "parthenogenetic"? Why, finally, does not the deep substance of our epidermis and epithelium, which absolutely more nearly resembles embryonic tissue than the structure of the pseudovarium does, give rise to young?

It may be replied, however, that the supposed "spermatic force" is exhausted by the repeated subdivisions of the germ-cell before it becomes a part of the deep epidermic tissue; for it is one condition of the hypothesis, that every successive generation or series of spontaneous fissions of the primary impregnated germ-cell must weaken the "spermatic force" transmitted to such successive generation of cells.

I presume, however, that the original "spermatic force" is at least as strong in a Man as in an *Aphis*. The average size of the embryo-cells in *Aphis* is at least not greater than in Man, and the specific gravities of their essential tissues are not very different; so that we may fairly assume that as many embryo-cells go to form a given mass of *Aphis* as of Man. In that case the impregnated embryo-cell must subdivide as often; and therefore the "spermatic force" must become as much exhausted in forming, say, a grain or a pound of *Aphis*, as in giving rise to the like quantity of human substance.

In his Lectures, Prof. Owen adopts the calculations taken by Morren (as acknowledged by him) from Tougard, that a single impregnated ovum of *Aphis* may give rise, without fecundation, to a quintillion of *Aphides*\*. I will assume that an *Aphis* weighs  $\frac{1}{1000}$ th of a grain, which is certainly vastly under the mark. A quintillion of *Aphides* will, on this estimate, weigh a quadrillion of grains.

He is a very stout man who weighs two million grains; consequently the tenth brood alone, if all its members survive the perils to which they are exposed, contains more substance than 500,000,000 stout men—to say the least, more than the whole population of China! And if the law cited above be correct, the "spermatic force" in each cell of an *Aphis* of this brood must be diminished 500,000,000 times as much as that of a single human cell; nevertheless the "spermatic force" of the *Aphis* cell is enough to impel it to the production of young, while that of the human cell is not!

When to these considerations I add, that it has been shown that the agamic propagation of the *Aphis* may, under proper conditions, be continued for four years without interruption, in which case the "spermatic force" in the later broods must stand in an infinitely minute ratio even to that contained in the cells of the tenth generation, the *reductio ad absurdum* by simple arithmetic, of the so-called explanation, appears to me to be sufficiently obvious.

For the sake of argument, however, I am willing still to suppose for a moment that agamogenesis does take place in consequence of the retention of a "spermatic force." But I must ask, how does this phrase constitute an explanation of the phenomena? Nothing is more common than the misuse of the word "force" on the part of those who are more versed in the phraseology, than trained in the severe methods, of physical science. The impatient inquirer every now and then calls in the aid of molecular force, or chemical

\* I have not thought it worth while to add, in the products of the generations preceding the tenth.

force, or magnetic force, or od-force, to account for the existence of a mass of phenomena which will not arrange themselves under any of his established categories—forgetting that a “force,” the conditions of whose operation (that is, whose laws) are undetermined, is but a scientific idol, at once empty and mischievous,—empty, because it is but a phrase without real meaning; mischievous, because it acts as an intellectual opiate, confusedly satisfying many minds and obstructing the progress of inquiry into the real laws of the phenomena. If we show that a fact is a case of a law, we explain that fact; but explanation by reference to an undefined “force,” of questionable existence, is simply ‘ignorance writ large.’

Now, how does the hypothesis fulfil the indispensable conditions of a genuine explanation? In the first place, what proof is there of the existence of such a force as “spermatic force.” All that we *know* is, that an ordinary ovum will not undergo those changes which constitute development without the contact of the spermatozoon. Hence it is concluded that some force contained in the spermatozoon is the efficient cause of all these changes. But what would be thought of the artillerist who should imagine he had explained the propulsion of a bullet by saying it was ‘trigger force’? Or to take an illustration from phenomena of a like order to those under discussion: a seed will not grow unless it is exposed to a certain amount of warmth and moisture; but have I explained the growth by saying that it is the effect of ‘heat and moisture force’ which becomes diffused through the seed?

The very existence of this “spermatic force,” then, is a gratuitous assumption; and if we seek for its laws of action, we find but two stated: first, that it becomes weakened by the successive divisions of the germ-cell; second, that “the force is exhausted in proportion to the complexity and living powers of the organism developed from the primary germ-cell and germ-mass.”

I have shown to what singular consequences the first assumption leads us; it remains only to consider the second. If it be true, the occurrence of agamogenesis in the animal kingdom must bear an approximatively inverse ratio to the complexity of the organization of the different groups. Let us examine one or two subkingdoms in this point of view. Among the *Annulosa*, the *Rotifera* and *Turbellaria* possibly possess it to a small extent; the *Nematoidea* do not possess it at all. Many *Trematoda* possess it; others, such as *Aspidogaster*, have nothing of the kind. The *Acanthocephala* are not known to possess it; the *Echinodermata* are regarded by Prof. Owen as possessing it, but their different families show every gradation from simple metamorphosis to something like agamogenesis. A few *Annelida* possess the power in a marked degree; in many, nothing of the kind is known. The *Nais* has it; the Earth-worm and the Leech have it not. Of the *Crustacea*, some, such as many *Branchiopoda*, exhibit it in the highest perfection; but no trace of it has yet been found in *Copepoda*, *Cirripedia*, *Pæcilopoda*, *Edriophthalmia*, or *Podophthalmia*. In the *Myriapoda* and *Arachnida* the process is not known: but we find it in the highest *Articulata*—the *Insecta*—and this not, so far as we know at present, in *Aptera* or *Orthoptera*, but in a few *Hemiptera*, *Hymenoptera* and *Lepidoptera*; and there is every reason to believe that it only occurs in isolated, though perhaps in many, genera of these orders. Take the *Mollusca* again: agamogenesis occurs in the *Polyzoa* and *Ascidiodia*, not in the *Bra-*

*chiopoda*. It is not known to occur in any of the *Lamellibranchiata*; and among the higher *Mollusca* the nearest approach to it is presented by the animal (whatever it is) which gives rise to the "Synapta-schnecken" (high Gasteropods), and by the Hectocoty-ligenous *Cephalopoda*.

After this simple statement of well-known facts, I need not remind even the tyro in zoology, that there is no evidence of an inverse relation between the occurrence of agamogenesis and complexity of organization.

I have hitherto, in the course of this argument, confined myself in the main to the development of *Aphis*; but it is only just to observe that the author of the hypothesis brings forward yet another original observation in support of his large generalization:—

"In the freshwater polype, the progeny of the primary impregnated germ-cell retained unaltered in that body, may set up, under favourable stimuli of light, heat, and nutriment, the same actions as those to which they owed their own origin; certain of the nucleated cells do set up such actions, those, *e.g.* in the *Hydra fusca*, which are aggregated near the adhering pedicle or foot; and the result of their increase by assimilation and multiplication is, to push out the contiguous integument in the form of a bud, which becomes the seat of the subsequent processes of growth and development; a clear cavity or centre of assimilation is first formed, which soon opens into the stomach of the parent; but the communication is afterwards closed, and the young hydra is ultimately cast off from the surface of the parent\*."—'Lectures,' 2nd ed. p. 124.

I have had occasion carefully to watch the process of gemmation not only in *Hydra*, but in many species of all the other subdivisions of the *Hydrozoa*; and I venture to assert that no such process as that described by Prof. Owen takes place in any one of them.

The bud is from the first in communication with the cavity of the body, of which it is a mere diverticulum, whose walls are a little thickened at the extremity. No special cell or group of cells can be discovered as the centres whence growth proceeds. No "integument" is pushed out by any thing beneath it; but the outer layer of the body of the animal thickens and grows *pari passu* with the growth of the bud. No especial accumulation of derivative germ-cells can be seen in any part of the body of any *Hydrozoon*; and before gemmation commences there is no distinguishable difference of texture between the part in which gemmation commences and any other portion of the body. Furthermore if a complex Hydrozoon, such as a *Physophora* or *Agalma*, be examined, it will be found that there is no histological distinction whatsoever between that part of the body which is to give rise to a free swimming generative zooid, and that which produces merely a bract, a tentacle, or a stomach.

In this case then, as in that of the *Aphis*, the hypothesis receives no support from, but is totally opposed by, facts; and I unreservedly adopt the conclusion (long since clearly and well expressed by Dr. Carpenter), that "spermatic force" is but a name without definite meaning, applied to that which is not proven to exist, and the assumption of whose existence, even, does not help us a single step towards the understanding of the wonderful phenomena of agamogenesis.

\* I have cited this passage from the 'Lectures' rather than from the work on "Parthenogenesis," as they may be supposed to contain the expression of the author's latest views,



Truly we may say, with Degeer (*l. c.* p. 129), "Les Pucerons sont des insectes bien capables de déranger tout système formé de génération, et de mettre en déroute tous ceux qui s'efforcent d'expliquer ce mystère de la nature."

But the question may be asked: if the "spermatic force" be a myth, what *is* the cause of the phenomena? Considering that the groundwork of modern physiology is not a score of years old, I do not think the confession of our inability to answer that question at present is any opprobrium to science.

When we know why, in a mass of tissue of identical structure throughout, one part becomes a brain, and another a heart, and a third a liver—when we can answer these every-day questions of the sphinx, we may attempt her more difficult riddles without running too great a risk of being devoured.

At the present time it seems to me well nigh hopeless to look for an explanation of these phenomena. Some such classification of them, however, as will indicate their analogies with other vital manifestations, may fairly be attempted, and, when successfully carried out, will prove the first step towards an explanation.

#### § 7. *Classification of the Phenomena of Agamogenesis.*

It does not seem to be very difficult to effect such a classification. In the course of the development of the total product of a single impregnated ovum (which, with Dr. Carpenter, I regard as the zoological individual), one of two things may occur: either all the living products may remain in connexion with one another, or they may become separated from one another. The former case I term *Continuous*, the latter *Discontinuous Development*.

In continuous development, the size may increase, the form and texture remaining unchanged—constituting simple *growth*; or, the size remaining unchanged, the form and texture may alter—constituting simple *metamorphosis*; or the two processes may be combined, as in all those changes which we term *gemmation*, without separation from the parent.

Discontinuous development differs from continuous only in this, that the products of the growth and metamorphosis of the embryo become separated into two or more portions, which when they retain their vitality independently are termed "zooids."

When the produced "zooid" is capable of development into an independent organism without the influence of an act of conjugation with another zooid, I term the process *agamogenesis*. The producing zooid may be devoid of sexual organs, as in the *Salpæ*, many *Hydrozoa*, many *Trematoda*—in fact, in the great majority of cases of agamogenesis.

I term the first producing zooid of the individual the *protozooid*; the produced zooids, *deuterozooids*. In some cases the deuterozooids acquire sexual organs, and give rise to ova and spermatozoa; but in others they produce new zooids: thus broods of *tritozooids*, &c., will be produced. When the producing or protozooid possesses no sexual organs, I think Prof. Owen's term of "*metagenesis*" might well be applied to the kind of agamogenesis; but where the protozooid possesses sexual organs, and its buds have all the histological characters of ova, then the process may fairly enough be termed *parthenogenesis*.

